HUMAN SOCIOBIOLOGY

by Michael J. Reiss

Abstract. Sociobiology is the scientific study of why organisms sometimes associate with other organisms. This paper surveys recent research on the reasons for altruism and aggression. It also considers the contributions an individual's genes and its environment make to its behavior, and it reviews functional theories for the evolution of cannibalism, polygamy, homosexuality, and infanticide in humans and other animals. Finally mention is made of the limited and generally negative attitude of sociobiology to religion.

Sociobiology, as a named discipline, dates from comparatively recently. Its birth came with the publication of E. O. Wilson's *Sociobiology: The New Synthesis* in 1975. This massive tome (as Mary Jane West-Eberhard noted in her review of it [1976], the book weighs five pounds) went on to become Harvard University Press's best ever selling book. While it may yet be premature to maintain that its influence will equal that of its illustrious predecessor after which it is named—*Evolution: The Modern Synthesis* by Julian Huxley (1942)—it certainly has given rise to what is by now a genuinely new discipline exciting considerable comment and controversy since its inception and with several of its own journals, for example, *Behavioral Ecology and Sociobiology* and *Ethology and Sociobiology*.

In this paper I will try to indicate what sociobiology is, and I will try to show the sort of problems that particularly interest sociobiologists. While the great majority of the research done by sociobiologists is on nonhumans, I will give several examples of the work done on humans. Some of the resultant conclusions are speculative and illustrate the difficulties of testing some of the theories proposed by sociobiologists.

Sociobiology is the systematic study of the biological basis of all social behavior. The problem of social behavior is of particular interest to

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evolutionary biologists as social behavior often includes altruism—the lowering of one's personal fitness at someone else's benefit. How, therefore, can altruism possibly evolve through natural selection?

Sociobiologists are interested in much besides altruism. In many species an understanding of the evolutionary pros and cons of sociality requires a detailed empirical knowledge of the patterns of agression shown within the species, of the different roles (fixed throughout life, as in many social insects, or dependent on age, as in most vertebrates) individuals adopt depending on their sex or social status, and of the range of environments in which the species lives. This empirical knowledge needs to be placed in as unified a theoretical framework as possible. Ideally, testable hypotheses should result, allowing the theoretical framework to be examined and improvements to be suggested.

ALTRUISM

One way in which Charles Darwin's genius manifested itself was in his habit of erecting counterarguments to his own theories. Having developed the theory of natural selection, he went on in *The Origin of Species* (1859) to consider how the sterile castes in many social insects could have evolved. Surely, it might be argued, such castes cannot have evolved by natural selection because the bearers of traits associated with sterility leave, by definition, no offspring. However, Darwin realized that sterility in such circumstances could evolve by a process he termed "family selection." For example, he pointed out that "breeders of cattle wish the flesh and fat to be well marbled together; the animal has been slaughtered, but the breeder goes with confidence to the same family" (Darwin 1859, 358). So sterility might, under certain circumstances, be favored if an individual's sterility was compensated by the extra number of descendants surviving to his or her relatives. This indeed is what seems to happen in social insects. For example, within a honeybee colony, the sterile female workers are typically the full sisters of the few fertile bees (males and females) that will give rise to future colonies. In a colony with tens of thousands of individuals, the loss of a few workers through the stinging of potential predators hardly matters. The safety and protection of the future reproductives is the paramount consideration.

In the African termite *Globitermes sulfureus* members of the soldier caste are literally walking bombs (Wilson 1978)! Huge, paired glands extend from their heads back through most of their bodies. When they attack ants and other enemies, they fire a yellow glandular secretion through their mouths; this congeals in the air and often fatally entangles the aggressive soldier termites themselves as well as their antagonists. The spray appears to be powered by muscular contractions in the abdominal wall, and the contractions are sometimes so violent that the gland explodes together with the abdomen, spraying the fluid and the soldier in all directions.

The name now given to this kind of altruism—where an individual performs an action which decreases its own fitness, but where this is more than compensated for by the increased fitness of its relatives—is kin selection (Smith 1964). The first steps in the determination of just how much benefit relatives have to receive to compensate an individual's altruism were taken separately by the geneticists J. B. S. Haldane and R. A. Fisher. Fisher (1930) was concerned with the evolution of distastefulness, the process by which nauseous flavors have been evolved as a means of defence. The problem is that predators frequently only realize that an individual prey is distasteful once they have killed the prey and have begun eating it. If predators learn to avoid such distasteful prey, then the prey species clearly benefits, but the individual evidently does not. This problem is enhanced when aposematism occurs, that is, where distastefulness is associated with striking coloration, as in many butterflies. It has been demonstrated that such colorations sometimes *attract* predators. Fisher realized that the gregarious habit of many aposematic prey supplies the possible answer:

> For, although with the [solitary] adult insect the effect of increased distastefulness upon the actions of the predator will be merely to make that individual predator avoid all members of the persecuted species, and so, unless the individual attacked possibly survives, to confer no advantage upon its genotype, with gregarious larvae the effect will certainly be to give the increased protection especially to one particular group of larvae, probably brothers and sisters of the individual attacked. The selective potency of the avoidance of brothers will of course be only half as great as if the individual itself were protected; against this is to be set the fact that it applies to the whole of a possibly numerous brood (Fisher 1930, 178).

Here Fisher, in his typical clipped manner, mentions that kin selection directed towards full sibs has only half the strength of individual selection. Similarly Haldane once remarked that he was prepared to lay down his life for two of his brothers or eight of his cousins! A full quantitative treatment of kin selection came only with W. D. Hamilton's seminal pair of papers (1964), *The Genetical Evolution of Social Behaviour I & II*, widely regarded as the founding papers of sociobiology. Hamilton was able to show that the condition for the spread of altruism through kin selection could succinctly be expressed in a simple equation:

$$\frac{b}{c} > \frac{1}{r},$$

where b is the benefit (in terms of Darwinian individual fitness) that accrues to the beneficiary of the altruism, c is the cost (again in terms of Darwinian individual fitness) that the altruist suffers, and r is the degree of relatedness between the two individuals. Also r is the proportion of their genes that the two individuals have in common *by virtue of identity of descent*. For example, in an outbred population of a sexually reproducing diploid species the degree of relatedness between a parent and his or her offspring is a half, between an uncle or aunt and a niece or nephew is a quarter, and between two first cousins, as Haldane knew, is an eighth.

Subsequent to Hamilton's original work there have been an enormous number of papers and books dealing with the precise quantitative predictions of kin selection theory, and minor modifications of Hamilton's simple rule are now known to apply under certain conditions (Cavalli-Sforza and Feldman 1978; Charlesworth 1978, 1980; Smith 1980). However, at worst, Hamilton's formula still provides an extremely accurate approximation to the conditions under which kin selection operates.

A second way in which altruism can evolve is by reciprocal altruism. The mechanism for this was first explicitly described by R. L. Trivers in 1971. Essentially reciprocal altruism is an example of "You scratch my back, I'll scratch yours." Perhaps the most convincing example occurs in male olive baboons, *Papio anubis* (Packer 1977). Craig Packer studied eighteen adult males in three troops at Gombe National Park, Tanzania, for more than 1100 hours. All males leave their natal troops and transfer to another troop before reproducing. This means that any one troop often contains a number of males unrelated to each other. Coalitions between unrelated males are sometimes formed in attempts to separate an opponent from an estrous female—olive baboons form exclusive consort pairs lasting for up to several days. If a pair of males do succeed in obtaining a female in this manner, only one of the two coalition partners mates with her. Attempts at enlisting a coalition partner can unambiguously be recognized: one individual, the enlisting animal, repeatedly and rapidly turns his head from a second individual, the solicited individual, towards a third individual, the opponent, while continuously threatening the third.

Packer saw twenty occasions when coalitions formed when the opponent was consorting with an estrous female. In six of these cases the formation of a coalition directed against the consorting male resulted in the loss of the female by the single opponent. In all six cases the female ended up with the enlisting male of the coalition ($p = 0.032$; two-tailed sign test); the solicited male generally continued to fight the opponent while the enlisting male gained access to the estrous female.

In each case the solicited male evidently risked injury from fighting the opponent while the enlisting male gained access to an estrous female.

The crucial fact that Packer discovered was that males sometimes reciprocated in joining coalitions at each other's requests. Individual males that most frequently gave aid were those that most frequently received aid. There was a strong correlation between the frequency with which adult males joined coalitions and the frequency with which they successfully enlisted coalition partners ($\zeta = 0.84$, $z = 2.87$, $p < 0.004$; Kraemer test, based on Spearman correlations). Furthermore, males have preferences for particular coalition partners based at least partly on reciprocation: for nine of the ten males who solicited other males on four or more occasions, the favorite partner in turn solicited the original more often than the average number of occasions that the partner solicited all adult males in their troop ($p = 0.022$; two-tailed sign test).

The third way in which altruism can theoretically evolve is by group selection. The first really detailed arguments in favor of group selection were put forward by V. C. Wynne-Edwards in 1962. Wynne-Edwards was primarily concerned with attempting to explain how population density is regulated. Populations, he argued, should not overexploit their food supplies, for such overexploitation would lead to reduced food yields and thus to lower reproductive success. As an example he described how the potential yield of many fisheries became drastically reduced when they were overfished, but could recover when catches were voluntarily restricted. Similar processes should apply, he argued, to animal populations, which should restrict their population density and rate of reproduction rather than endanger their food supply.

As Wynne-Edwards's theory depends on the assumption that individuals do *not* always maximize their own reproductive success, it was necessary to extend evolutionary theory to account for this. Wynne-Edwards argued that groups containing individuals who reproduce too fast, so that the recruitment rate persistently tended to exceed the death rate, must have repeatedly exterminated themselves by overtaxing and progressively destroying their food sources. Prudent groups, where altruistic individuals restrained their reproduction would outlive more selfish groups, and so come to predominate.

These then are the three major theories put forward to explain the existence of altruism—kin selection, reciprocal altruism, and group selection. What are their relative importances in nature?

Most theoreticians, with some notable exceptions, have accorded Wynne-Edwards's theory of group selection a poor welcome. Group selection faces a fundamental theoretical problem as pointed out by

John Maynard Smith (1964). Consider a prudent group whose members are reproducing submaximally due to group selection. Suppose now that a mutation arises which causes its holder to reproduce maximally. Even if such a group now becomes more prone to extinction as group selection requires, the altruistic individuals within it would, by definition, produce fewer surviving descendants than the other group members bearing the new mutation. Consequently, selection acting *within* the group would tend to eradicate the altruistic trait. Group selection only becomes important when two conditions are fulfilled: first, that selfish groups go extinct *much* more quickly than prudent groups, and second, that little migration takes place between groups. When migration becomes common, selfish individuals tend to move between groups before groups go extinct. The available data on animal migration and demography suggest that group selection, certainly in vertebrates, is unlikely to be important (Smith 1976).

Reciprocal altruism is on a firmer theoretical footing but appears comparatively rare within species. As Trivers realized, a fundamental problem with reciprocal altruism is the possibility of cheating: "You scratch my back, but then I run away." Probably the most convincing nonhuman example of reciprocal altruism is the study cited above by Packer on olive baboons, although even here it is possible that at least some of the males may have been related, which would implicate kin selection. The preconditions for the evolution of reciprocal altruism are similar for the operation of kin selection: long lifetime, low dispersion rate, and mutual dependence. These make it difficult in any one case to distinguish between the alternatives of kin selection and reciprocal altruism. In his original paper Trivers gave as examples of reciprocal altruism the convincing cases of so-called interspecific cleaning symbioses. These cannot have evolved by kin selection, as cleaning (the altruistic act) is performed by members of one species for the benefit of members of another.

In such cleaning symbioses one organism (e.g., the wrasse, *Labroides dimidiatus*) cleans another organism (e.g., the grouper, *Epinephelus striatus*) of ectoparasites (e.g., caligoid copepods), sometimes entering into the gill chambers and mouth of the host to do so. About fifty species of fish, as well as six species of shrimp, are known to be cleaners. Innumerable species of fish serve as hosts. Stomach analyses of cleaner fish demonstrate that they vary greatly in the extent to which they depend on their cleaning habits for food, some apparently subsisting nearly entirely on a diet of ectoparasites. Likewise, stomach analyses of host fish reveal that cleaners differ in the rate at which they end up in the stomachs of their hosts, some being almost entirely immune to such a fate. It is a striking fact that there seems to be a strong correlation between the degree of dependence of the cleaner on the cleaning way of life, and immunity to predation by hosts. Cleaning habits have apparently evolved independently many times. One remarkable feature is the way in which fish avoid eating their cleaners. Why, asks Trivers, does a large fish not end a cleaning bout by swallowing the cleaner—thus earning an easy meal? Trivers argues that cleaners are worth more to hosts alive than dead. If a host eats a cleaner it may have difficulty finding another when it needs to be cleaned again. Just how important cleaners are to their hosts has been demonstrated in experiments where cleaners are removed (Limbaugh 1961, Feder 1966). Within a few days the number of fish in the area is drastically reduced. Within a couple of weeks almost all except territorial fish disappear, and many of these develop white fuzzy blotches, ulcerated sores, and frayed fins. Clearly, once a fish's primary way of dealing with ectoparasites is by being cleaned, it is quickly vulnerable to the absence of the cleaners.

In the animal kingdom as a whole, kin selection appears to be the most important selective force maintaining altruism. In a very large number of social species convincing data exist to show that closer relatives receive correspondingly greater aid (Yamada 1963, Kurland 1977, Massey 1977, Sherman 1977, Kaplan 1978, Hrdy 1977), and in a few cases Hamilton's predicative equation for the evolution of kin selection has been tested and at least partially verified (West-Eberhard 1967, Emlen 1978). A particularly elegant form of kin selection was found in saturniid moths by A. D. Blest (1963). Consider two types of insect, one cryptic (difficult for a predator to find) and palatable, the other aposematic (easy for a predator to find) and distasteful, and both subject to predation. The longer that a cryptic insect survives after reproducing, the greater the chances that it will be found by a predator who will *learn* to recognize and find other individuals of the species. Postreproductive survival evidently prejudices the survival of the other members of the species including close relatives. The contrary argument applies to the aposematic insect. Predators will learn to *avoid* such prey. The postreproductive survival of an aposematic insect, then, should favor the survival of its siblings. Blest's predictions were fulfilled by the data he collected on Barro Colorado Island in the Panama Canal Zone. The aposematic species had postreproductive life spans several times those of the cryptic species.

So much for nonhumans. What about altruism in man? Some anthropologists, for example, M. Sahlins (1977), have argued that no system of human kinship relations is organized in accord with the genetic coefficients of relationship, as predicted by sociobiologists. Actually this is not so. For example, in a detailed analysis of the intra- and inter-group degrees of relatedness in a Yąnomamö ax fight, Napoleon Chagnon and P. E. Bugos, Jr. (1979) found that the alliances formed were strikingly close to those predicted by the most crude application of kinship theory—that aid should increase as the degree of relatedness between two individuals increases. (The application of kinship theory is crude because this prediction ignores possible variation in the benefit/cost part of Hamilton's equation.)

That the Yą̧nomamö fight alongside their close relatives is hardly surprising. All of us know that kinship is important in human social relationships. One step forward taken by sociobiology is to make quantitative predictions about the extent to which kin selection favors relatives. Sadly, however, the required data are difficult to collect from ants and wasps, let alone from humans. Nevertheless, it is natural to ask whether kin selection is responsible for the capacity for altruism in humans. In other words, as E. O. Wilson puts it (1978), do the emotions we feel, which in exceptional individuals may climax in total self-sacrifice, stem ultimately from hereditary units that were implanted by the favoring of relatives during our evolutionary history? This suggestion gains some support from the probable fact that during most of mankind's history the predominant social unit was the immediate family and a tight network of other close relatives.

In a few societies fathers take little or no interest in their wife's children but direct their paternal interest towards their sister's children. As one's sisters' children are less closely related to one than one's own offspring, this practice appears paradoxical. Consider, however, what happens when there is a good deal of uncertainty about paternity. One's sisters may only be half-sisters, but they and their children are indubitably one's true kin. On the other hand, one's wife's children may often be unrelated to one, if adultery is rife. A review of the ethnographic literature provides some support for the expectation that it is in precisely those societies in which there is the greatest uncertainty about paternity that men divert a substantial part of their parental care to their nephews and nieces (Alexander 1974, Kurland 1978).

Humans are perhaps unique in that the female shows a prolonged menopause. It has been suggested that postmenopausal women may exhibit kin-selected altruism.[1] The idea is that, freed from their own reproductive constraints, such women have the time to help in the care and rearing of their other relatives including, for example, their grandchildren.

One other possible form of altruism is worth mentioning—homosexuality, forbidden as it is by mainstream Judaism and Christianity. A. C. Kinsey's classic studies concluded that as many as two percent of American women and four percent of men were exclusively homosexual, while thirteen percent of men were predominantly homosexual for at least three years of their lives (Kinsey, Pomeroy, and Martin 1948; Kinsey et al. 1953). Homosexual behavior of one form or another is common in virtually all other cultures and has been permitted or approved in a number of societies: in classical Athenian, Persian, and Islamic societies, in late republican and early imperial Rome, in the urban, Hellenistic cultures of the Middle East, in the Ottoman Empire, and in feudal and early modern Japan.

Wilson, H. T. Spieth and Trivers have suggested that homosexuality is normal in a biological sense, and that it is a distinctive beneficient behavior that evolved as an important element of early human social behavior (Wilson 1978, Trivers 1974).[2] Studies of twins suggest that homosexuality has a genetic basis (Heston and Shields 1968). This brings us to the nub of the problem. How can genes predisposing their carriers towards homosexuality spread through the population if homosexuals have fewer than the average number of children? Although there is little supporting evidence, as Wilson fully admits, the close relatives of homosexuals could have had more children as a result of their presence. Freed from parental obligations, homosexuals would have been in a position to operate with special efficiency in assisting close relatives. They might further have taken the roles of seers, shamans, artists, and keepers of tribal knowledge—and there is some evidence for this (Weinrich 1976, Reiche and Dannecker 1977). If the relatives of homosexuals benefitted thus, the genes these individuals shared with the homosexual specialists would have increased at the expense of alternative genes. Inevitably, some of these genes would have been those that predisposed individuals towards homosexuality. A proportion of the population would consequently always have the potential for developing homophilic preferences.

While some kin selection evidently operates on humans, reciprocal altruism is probably of particular importance. Reciprocation among distantly related or unrelated individuals is the key to much of human society. As Wilson writes: "The 'altruist' expects reciprocation from society for himself or his closest relatives. His good behavior is calculating, often in a wholly conscious way, and his maneuvers are orchestrated by the excruciatingly intricate sanctions and demands of society. The capacity for [reciprocal] altruism can be expected to have evolved primarily by selection of individuals and to be deeply influenced by the vagaries of cultural evolution. Its psychological vehicles are lying, pretense, and deceit, including self-deceit, because the actor is most convincing who believes that his performance is real" (Wilson 1978, 155-56).

NATURE/NURTURE

Each of us is a product of the interaction between our genetic makeup and our environment. An important question is to what extent is human social behavior genetically determined? Although the range of human cultures seems vast, all versions of human social behavior together form only a tiny fraction of the realized organizations of all the social species on this planet (see Wilson 1978). Having said that, it is worth clarifying exactly what is meant by a genetically determined trait. It is a trait that differs from other traits in part as a result of one or more distinct genes. To say that blue eyes are inherited is not very meaningful as blue eyes are a product of an interaction between genes and the largely physiological environment that brings final coloration to the irises. But to say that the *differences* between blue and brown eyes is based at least partly on differences in genes is a meaningful statement, because it can be tested. What are the eye colors of the parents and their relatives? These data can then be incorporated into genetic models based on the assumption that only a pair of alleles at a single gene locus on one of the chromosomes is responsible for the difference. If the data reject such a simple model, then more complicated possibilities can be suggested involving larger numbers of genes and interactions between them. In the case of the most complex traits, hundreds of genes are sometimes involved, and their degree of influence can ordinarily only be measured approximately and with the aid of sophisticated mathematical techniques. Nevertheless, when the analysis is performed it leaves little doubt as to the presence and rough magnitude of the genetic influence.

Human social behavior can be considered in this way, first by comparison with the behavior of other species and then by studies of variation among and between human populations. Convincing evidence of a strong level of genetic determinism in some of our social traits comes when we compare ourselves with the rest of the animal kingdom. Some of our traits are shared with many of the great apes and monkeys which, on the grounds of anatomy and biochemistry, are obviously our closest living evolutionary relatives. These traits include the following.

1. Our intimate social groupings contain on the order of ten to one hundred adults, never just two as in most birds and marmosets, or up to thousands as in many fish and insects.

2. Males are larger than females. Within a number of mammalian taxa (primates, antelopes and seals) it is known that the average number of females consorting per successful male parallels closely the degree of sexual dimorphism in body weight within the species. This is as expected. The greater the competition between males for access to females, the greater the advantage of increased male size. Men are not very much larger than women. When the degree of sexual dimorphism in body weight in humans is plotted on a curve based on other primates,

the predicted average number of females per successful male turns out to be more than one but less than three (Clutton-Brock, Harvey, and Rudder 1977; Alexander et al. 1979; Harcourt et al. 1981; Martin and May 1981). This fits with common observation; we are a mildly polygynous species.

3. Children have a long period of social training, first from the mother, then to an increasing degree by association with other children, usually of the same age and sex.

4. Social play is a strongly developed activity featuring role practice, mock agression, sex practice, and exploration.

At the next, finer level of classification, we are distinct from monkeys and apes in ways that can adequately be explained only as a result of a unique set of human genes. In 1945 the anthropologist G. P. Murdock listed the following characteristics that have been recorded in every culture known to history and ethnography: age-grading, athletic sports, bodily adornment, calendars, cleanliness training, community organization, cooking, cooperative labor, cosmology, courtship, dancing, decorative art, divination, division of labor, dream interpretation, education, eschatology, ethics, ethnobotany, etiquette, faith healing, family feasting, fire making, folklore, food taboos, funeral rites, games, gestures, gift giving, government, greetings, hair styles, hospitality, housing, hygiene, incest taboos, inheritance rules, joking, kin groups, kinship nomenclature, language, law, magic, marriage, mealtimes, medicines, obstetrics, penal sanctions, personal names, population policy, postnatal care, property rights, propitiation of supernatural beings, puberty customs, religious ritual, residence rules, sexual restrictions, soul concepts, status differentiation, superstitions, surgery, tool making, trade, visiting, weaving, and weather control.

As Wilson points out, few of these unifying properties can be interpreted as the inevitable outcome of either advanced social life or high intelligence. It is easy to imagine nonhuman societies with members more intelligent and complexly organized than ourselves, yet lacking a majority of the above qualities, and possessing others—for example body licking, cannibalism, communal nurseries, euthanasia, mutual regurgitation, and sterile workers, as already exist in the social insects.

One of the items in Murdock's list is incest taboos. The universality of incest taboos has long fascinated anthropologists, although the details of what degree of inbreeding is permitted in humans vary between societies. Mother-son, father-daughter, and brother-sister marriages are forbidden virtually everywhere. Beyond this there is great variability. There may be no taboo group beyond the nuclear family, or there may be literally thousands of theoretically forbidden mates. First-cousin marriages are forbidden in some societies but are obligatory in many others.

There is a simple biological reason why incest avoidance is a good thing—inbreeding depression (Crow and Kimura 1970). In many animals (with some notable exceptions[3]) mating between close relatives leads to reduced fertility and decreased viability of offspring. Data from humans are understandably rare, but nevertheless emphatically convincing. Among 161 children born to a sample of Czechoslovakian women where the father of the child was the brother, son, or father of the woman, 15 were stillborn or died within the first year of life and more than 40 percent suffered from various physical or mental defects including severe mental retardation, dwarfism, heart and brain deformities, deaf-mutism, and urinary-tract abnormalities. By contrast, 95 children born to the same women through nonincestuous relations were as normal as the population at large (Seemova 1972). Evidence of inbreeding depression in less extreme cases comes from a study of the chest sizes of men born in the Parma Province of northern Italy between 1892 and 1911 (Barrai, Cavalli-Sforza, and Mainardi 1964). The closer the degree of relatedness between the parents, the smaller the mean chest girth. Further studies have demonstrated depression effects in overall size, neuromuscular ability, and academic performance (Schull and Neel 1965).

Evidently incest in humans is biologically disadvantageous—both to the parents, particularly the mother who will inevitably have invested considerable energetic resources in the offspring once conceived, and to the resultant son or daughter. How then is incest avoided? One way is through incest taboos, although many social scientists have been or still are curiously reluctant to concede that natural selection against inbreeding might be relevant to the human phenomenon of incest avoidance (see Leach 1982). Interestingly, however, incest taboos do not accord perfectly with the biological predictions of inbreeding avoidance. In the *majority* of the marriage-types forbidden by the Church of England the parties are unrelated—for example husband and wife's sister. In addition, there is a second way in which incest is avoided. At least regarding brother-sister incest there is good reason to believe that inbreeding would be unlikely even in the absence of a culturally imposed taboo. The evidence for this comes from children raised *like* brothers and sisters, but between whom no barriers of biological kinship or cultural incest taboos exist.

Studies of young people raised on Israeli kibbutzim have revealed the remarkable fact that they do not marry within their rearing groups (Spiro 1958, Shepher 1971). The critical factor is very clearly that the children are raised together from an early age, since the only exceptions involved pairs who had been separated from one another for a large part of their childhood. The records of thousands of married adults reveal not a single marriage between a man and a woman reared together throughout childhood!

If rearing boys and girls together prevents mutual sexual interest, it should normally function as an effective outbreeding mechanism. In most circumstances, including those in which most hominoid evolution presumably took place, children reared in very close proximity are likely often to be kin, and the mechanism will function to assure outbreeding. Interestingly in the practice of *Shim-pua* marriage in Taiwan (Wolf 1970), the couple is wed as children and reared together. Such couples have more difficulty consumating their marriages, more extramarital affairs, more divorces, and fewer children than do couples whose marriages are arranged postpubertally.

AGGRESSION

Humans are aggressive. We are also territorial in that we defend our land and our possessions from each other. Part of man's problem is that his intergroup responses are still crude and primitive, inadequate for the extended extraterritorial relationships that civilization has thrust upon him. The unhappy result is what Garrett Hardin has defined as tribalism in the modern sense. "Any group of people that perceives itself as a distinct group, and which is so perceived by the outside world, may be called a tribe. The group might be a race, as ordinarily defined, but it need not be; it can just as well be a religious sect, a political group, or an occupational group. The essential characteristic of a tribe is that it should follow a double standard of morality—one kind of behavior for in-group relations, another for out-group" (Hardin 1972, 39). Xenophobia becomes a political virtue. The treatment of nonconformists within the group grows harsher.

There was a time when ethologists thought not only that humans were aggressive but also that they were uniquely and unnaturally so (e.g., Lorenz 1966). Actually this is not so. We are far from being the most violent species. Spotted hyenas (Kruuk 1972), lions (Schaller 1972, Bertram 1975), langur monkeys (Hrdy 1977), and many invertebrates (Wilson 1975) are more violent than we are and engage in lethal fighting, infanticide, and cannibalism at a rate far above that found in human societies. Chimpanzees (Goodall 1979) and spotted hyenas even clash in deadly battles virtually indistinguishable from primitive human warfare. Here is an account by Hans Kruuk over a dispute between hyenas:

> The two groups mixed with an uproar of calls, but within seconds the two sides parted again and the Mungi hyenas ran away, briefly pursued by the Scratching Rock hyenas, who then returned to the carcass. About a dozen of the Scratching Rock hyenas, though, grabbed one of the Mungi males and bit

> him wherever they could—especially in the belly, the feet and the ears. The victim was completely covered by his attackers, who proceeded to maul him for about 10 min while their clans fellows were eating the wildebeest. The Mungi male was literally pulled apart, and when I later studied the injuries more closely, it appeared that his ears were bitten off and so were his feet and testacles, he was paralyzed by a spinal injury, had large gashes in the hind legs and belly, and subcutaneous hemorrhages all over.... The next morning I found a hyena eating from the carcass and saw evidence that more had been there; about one-third of the internal organs and muscles had been eaten. Cannibals! (Kruuk 1972, 256).

One human culture where cannibalism was rife was in ancient Mexico. Here there was little of the large game that flourished on the plains of Africa and Asia. Furthermore, the Aztecs failed to domesticate animals as significant sources of meat. As the number of people increased, the Aztec ruling class was still able to enjoy such delicacies as turkeys, ducks, deer, rabbits, fish, and dogs. But animal flesh was virtually eliminated from the diets of the less fortunate who were occasionally reduced to eating clumps of algae skimmed from the surface of Lake Texcoco. The situation was partially relieved by cannibalizing the victims of human sacrifice. As many as 15,000 people a year were being consumed in the Valley of Mexico when Cortez entered. The conquistadors found 100,000 human skulls stacked in neat rows at Xocotlan and another 136,000 at Tencochtitlán. According to the priests, such sacrifices were approved by the gods. Temples were erected where elaborate rituals were performed. Once their hearts had been removed, the victims were butchered and their parts distributed and eaten. The fortunate eaters were probably the groups with the greatest power—the nobility, their retainers, and the army (Harner 1977, Harris 1977).[4]

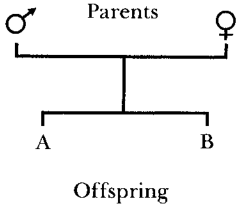
A straightforward application of sociobiological theory predicts that in humans male-male interactions should be more aggressive than female-female interactions (Darwin 1871, Trivers 1972). Ultimately this is because (as in most species) males are capable of siring more offspring than are females. Consequently reproduction is determined more by the number of women than by the number of men. So men are more competitive than women.

Competition between men for access to women is indeed a common cause of aggression. For example, in the Yąnomamö displays of masculinity, such as fighting prowess and *waiter* (ferocity), are admired by the women, and particularly aggressive men have an advantage both in soliciting the sexual favors of large numbers of women and in depressing the temptation of other men to seduce their wives. As Chagnon relates: "In investigating scores and even hundreds of different fights and village fissions or relocations, I would ask the Yąnomamö: 'Why did you fission there?' or 'What caused that fight?' Patiently, and slowly, my informant would sigh and say: 'Women!' If the informant was new and had never worked with me before, the answer would be somewhat more animated, and the informant astonished: 'What? Don't ask such a stupid question! It is women! Women! We fight over women!" (Chagnon 1979, 87). In the Yąnomamö younger men frequently attempt to seduce the wives of other men and seize every opportunity to approach the women when their husbands are not around. Men who go on several-day hunting trips, for example, keep their ears close to the ground when they return to pick up any telltale gossip that suggests infidelity on the part of their wives and often beat them soundly if there appears to be substance to the rumors. The wronged husband usually challenges the suspected lover to a club-fight as well. Such fights rapidly escalate and involve large numbers of the village men, who take sides with close kin (Chagnon and Bugos 1979). One quarter of all Yąnomamö men die in fights.

Sex and Reproduction

Theories about reproduction lie at the core of evolutionary biology and sociobiology. To a sociobiologist individuals exist only to pass their genes on to succeeding generations, either by themselves or via their relatives.

It is easy to assume that reproduction is in the offspring's interest. Sociobiology claims that this is an oversimplification (Trivers 1974, Parker and MacNair 1978). In sexually outbreeding species, parents and offspring are not genetically identical. Thus there is a conflict of interest between them. At some stage in a parent's investment in an offspring the parent has, on an evolutionary timescale, to "choose" whether to continue investing in its present offspring, A, or whether to start investing in another (second) offspring, B. (See the following diagram.)



Now each parent is related equally to A and B. A, however, is more related to itself than it is to B. Consequently, while the parents have the interests of A and B equally at heart, A is more interested in itself than in B.

How is this conflict of interest likely to manifest itself? Well, A should want more parental investment than the investing parents are prepared to give. Trivers (1974) suggested that this might be the explanation for weaning conflict in mammals, as such conflict occurs when the offspring wants more parental investment than the parent is prepared to give. A species where this is predicted *not* to be the case is the nine-banded armadillo. In this species young are always born in litters of identical quadruplets! Here, each offspring is just as related to its littermates as it is to itself. Consequently there should be no sib-sib competition for access to parental resources, or any other for that matter. This prediction has been around since at least 1976 (Dawkins 1976), but so far as I know nobody has yet undertaken the required study.

N. Blurton Jones (1978) has pointed out that parent-offspring conflict might be the explanation for a previously unexplained phenomenon in humans, namely that offspring birthweight is on average suboptimal in the sense that larger than average offspring survive better than average. Heavier babies would, of course, require more parental investment. There is, however, a simpler explanation. Larger than average babies might result in complications at birth, leading, in societies with only primitive obstetrics, to the death of the baby as well as the mother.

There are more dramatic examples of a genetic conflict of interests than suboptimal birthweights and weaning tantrums. In lions infanticide is rife. Detailed studies in the Serengeti and Ngorongoro of lion social organization by Brian Bertram (1975) have revealed the following story. Lions live in prides, the permanent social units of adult females, with their accompanying cubs and attached adult males. Most prides contain five to nine adult females and two or three adult males. The adult females are related to one another—indeed communal suckling occurs—but are unrelated to the adult males. Males never breed in their natal group but, like Packer's olive baboons (1977), must transfer from the group in which they were born before they can breed. Lions are the most sexually dimorphic species in the cat family, with males 50 percent heavier than females. This is presumably due to the considerable importance attached to the results of male-male fights. These occur when one group of adult males tries to take over a pride from another group of adult males. Often they succeed, and so prides have a rapid changeover of adult males—once every two to three years on average. Bertram found that the takeover of a pride by a new group of males often leads to an increase in cub mortality. Occasionally adult males are seen to kill and even eat cubs which will have been sired by the previous resident males. Of the 50 percent of cubs who died where Bertram could establish the cause of death, half died as a result of starvation and half through infanticide. Considering the obvious difficulties in establishing it with confidence as the cause of death, infanticide is evidently common in lions. Why?

The crucial point seems to be that when their cubs are killed, lionesses come back into estrus more rapidly than if they have first to wean their cubs, which happens on average at eight months of age. Apparently infanticide reduces the time that the males have to wait before they can sire any young.

This type of infanticide has also been observed in langurs (Hrdy 1977), gorillas (Fossey 1981), and redtail monkeys (Struhsaker 1978). In langurs an intriguing female strategy has evolved to reduce the chances of infanticide happening. After a new male has taken over a troop of female langurs, those of the females that are pregnant may show a false estrus resulting in copulations. These copulations lead to no conceptions, but the females naturally give birth subsequently to the young with which they were pregnant at the time of the false estruses. The data are as yet inconclusive, but this strategy may serve to trick the new male into assuming that the offspring are his. Consequently the level of infanticide is reduced to the female's advantage, but the male's disadvantage.

Infanticide in lions and langurs is in a sense unsurprising. The new males are unrelated to the young they kill. In humans, however, it appears that in some cases mothers will kill their own offspring. According to a demographic survey by W. T. Divale (1972) of over 600 primitive societies, there is a remarkable imbalance in the ratios of boys to girls, with an average ratio of 150:100. Divale argues that many societies follow a practice of overt female infanticide. Daughters are suffocated or simply left unattended in the bush. But more often the infanticide is covert—the discrepancy between female and male infant mortality rates usually results from a neglect of infant care, rather than from a direct assault on the female baby's life. Even a slight sex-difference in a mother's responsiveness to her childrens' cries for food or protection might cumulatively lead to imbalance in adolescent sex ratios.

Why, though, is female infanticide apparently more common than male infanticide? The answer seems to be that postinfant males are more likely, both through war and disease, to die than are postinfant females. The fact that the most successful males sire far more descendents than the most successful females (Darwin 1871, Trivers 1972) means that female-biased infanticide should be particularly pronounced in the *upper* classes, as parents in these classes will gain more descendents through their sons than through their daughters (Dickemann 1979).

In precolonial and British India, the upward social flow of daughters by marriage to higher ranking men (termed hypergamy) was sanctified by custom and religion, while female infanticide was practiced routinely by the upper castes. After all, in a such a schema of things, whom are the females of the upper castes to marry? The Bedi Sikhs, the highest ranking priestly subcaste of the Punjab, were known as *Kuri-Mar*, the daughter slayers. They destroyed virtually all daughters and invested everything in raising sons who would marry women from lower castes. In pre-revolutionary China female infanticide was commonly practiced by many of the social classes, with essentially the same effect as in India—a socially upward flow of women accompanied by dowries, a concentration of both wealth and women in the hands of the middle and upper classes, and near exclusion of the poorest males from the breeding system.

Human infanticide need not be sex-specific. In many societies there is a birth-spacing mechanism of lactational anovulation, reinforced by taboos against sexual intercourse for some time after birth (Murdock 1965). The duration of the taboo period varies considerably, as does the faithfulness with which it is observed. The most common duration is about six months. In practice the mechanisms of birth spacing do not guarantee complete avoidance of competition between successful infants detrimental to the survival prospects of one or both. Two dependent infants can be a severe strain on the resources of a mother lacking modern technological support. Many people the world round routinely sacrifice one of a pair of twins unless unusually favorable circumstances suggest that both can be reared and when single births occur too close together, mothers often resort to infanticide. One Yąnomamö mother told Chagnon that she had been obliged to kill her latest baby because it would have taken milk away from her unweaned two-year-old son (Chagnon 1968). Detailed demographic surveys (controlling for the relevant confounding variables) demonstrate statistically that the older a first child is at the birth of a second, the more chance the second has of surviving (Knodel 1968).

There is another interesting parallel between lions and humans worth mentioning—and that is the relatively low probability in each species that a mating has of leading to conception. In lions, estrus lasts two to four days and matings occur *on average* every 15 minutes. Yet only 20 percent of estruses result in conception. Typically 1500 copulations are required per birth! Bertram (1975) provided the first functional explanation for this extraordinary low fertility. He suggested that this leads to less selective pressure among the males within the pride to compete for access to estrus females. Serious competition among the pride males, he reasoned, would be disadvantageous to females because it would result in the injury or death of these males; this in turn would cause more frequent changeovers of male groups in possession of the pride, as such changeovers occur more often in prides with few adult males. Such changeovers are disadvantageous to the adult females due to the aforementioned practice of infanticide by the new adult males.

Humans are remarkable in that women lack an estrous period and may mate at any time during their lives from puberty onwards. Most other female mammals mate only during a brief estrous period occurring about the time of ovulation. Humans are unusual among primates, though by no means unique, in that fathers often invest heavily in their young. In many mammals adult females are left to rear their young, but in humans, of course, fathers may invest considerably in their offspring both in terms of time and energy. The number of attempts to explain why women lack estrous periods is legion (Benshoof and Thornhill 1979). A recent contribution is due to two sociobiologists, R. D. Alexander and K. M. Noonan (1979). They suggest that sexual advertisement of ovulation in women might result in males being less likely to invest in the resultant offspring for two reasons. First, competing males might be attracted to the female. Once more than one male mated with her, none would be very confident that the children were his. Second, occasional estrous periods might allow males, after a brief time of guarding while the female was receptive, to seek copulations with *other* females who would compete later with the first female for the male's potential care.

Alexander and Noonan suggest thus that, in evolutionary terms, concealment of ovulation evolved in humans because it enabled females to force desirable males into consort relationships long enough to reduce their likelihood of success in seeking other females, and simultaneously raised the male's confidence of paternity by failing to inform other, potentially competing males of the timing of ovulation. If these events occurred in a situation in which parental care was valuable, but not (in the absence of concealed ovulation) sufficiently valuable to offset philandering, and in which desertion was frequent when confidence of paternity was low, they could tip the balance, making increased parental investment profitable to males.

CONCLUDING DISCUSSION

I shall leave the question of ethics and religion almost entirely to others, but I would like just to mention sociobiology's attitude to religion.

Sociobiology is a reductionist science (Peacocke 1979 and 1982). When Wilson wrote *Sociobiology* he envisaged that ethology and comparative psychology would both be cannibalized by neurophysiology and sensory physiology from one end and sociobiology and behavioral ecology from the other. Similarly Wilson sees anthropology and sociobiology as the last biological sciences fully to come under the umbrella of Darwinian evolutionary biology. Religion, for example, is assumed biologically to be adaptive—see for instance the earlier cited case of Aztec cannibalism (Harner 1977, Harris 1977). Briefly to consider one type of religion, belief in an active and moral God who created the world is held by 92 percent of the 13 societies where more than 36 percent of the subsistence comes from herding, by 82 percent of the 28 societies where 26 to 35 percent of the subsistence comes from herding, by 40 percent of the 20 societies where 16 to 25 percent of the subsistence comes from herding, and by only 20 percent of the 5 societies where 6 to 15 percent of the subsistence comes from herding (Lenski and Lenski 1970). It can be argued that the intimate relation of the shepherd to his flock provides a microcosm which stimulates deeper questioning about the relation of man to the powers that control him or, more simply, that such societies have the time to invent religions.

A quite distinct theory for the evolution of human culture including religion is advanced by Richard Dawkins. Dawkins suggests that not only animals (strictly their genes) reproduce, so do "memes."

> Examples of memes are tunes, ideas, catch-phrases, clothes fashions, ways of making pots or building arches. Just as genes propagate themselves in the gene pool by leaping from body to body via sperms or eggs, so memes propagate themselves in the meme pool by leaping from brain to brain via a process which, in the broad sense, can be called imitation. If a scientist hears, or reads about, a good idea, he passes it on to his colleagues and students. He mentions it in his articles and his lectures. If the idea catches on, it can be said to propagate itself, spreading from brain to brain. As my colleague N. K. Humphrey neatly summed up an earlier draft of this chapter: "... memes should be regarded as living structures, not just metaphorically but technically. When you plant a fertile meme in my mind you literally parasitize my brain, turning it into a vehicle for the meme's propagation in just the way that a virus may parasitize the genetic mechanism of a host cell. And this isn't just a way of talking—the meme for, say, 'belief in life after death' is actually realised physically, millions of times over, as a structure in the nervous system of individual man the world over."
>
> Consider the idea of God. We do not know how it arose in the meme pool. Probably it originated many times by individual "mutation." In any case, it is very old indeed. How does it replicate itself? By the spoken and written word, aided by great music and great art. Why does it have such high survival value? Remember that "survival value" here does not mean value for a gene in a gene pool, but value for a meme in a meme pool. The question really means: What is it about the idea of a god which gives it its stability and penetrance in the cultural environment? The survival value of the god meme in the meme pool results from its great psychological appeal. It provides a superficially plausible answer to deep and troubling questions about existence. It suggests that injustices in this world may be rectified in the next (Dawkins 1976, 206-7).

Finally, I have yet to meet or hear of a sociobiologist who believed that because a human behavior has evolved, it is necessarily desirable (Parker 1978): Infanticide, murder, and rape may be adaptive biologically without being inevitable. It is a mistake to confuse what is with what ought to be.

NOTES

1. I do not know who first suggested this. The idea is mentioned by D. P. Barash (1977). The possible existence of a postreproductive phase in the females of other mammals in considered by E. C. Jones (1975).

2. For H. T. Spieth, see his personal communication to E. O. Wilson (1975, 555).

3. For example, there is evidence that in Père David's deer, inbreeding depression, uniquely in ungulates, does not occur. This may be related to the fact that all of today's Père David's deer are descendents of a small stock kept in the Imperial Chinese Gardens for at least two thousand years. During this time repeated inbreeding must have occurred. From laboratory experiments it is known that, as theory predicts, repeated inbreeding can reduce the magnitude of inbreeding depression. (See Ralls, Brugger, and Ballou 1979.)

4. For other interpretations of Aztec cannibalism see Coe (1978) and Price (1978).

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